ZooKeys 864: 99–109 (2019)
doi: 10.3897/zookeys.864.35271
http://zookeys.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
ZooKeys
Launched to accelerate biodiversity research

A new genus and species of berothids (Insecta, Neuroptera) from the Late Cretaceous Myanmar amber

Qiang Yang[1], Chaofan Shi[2], Dong Ren[3]

1 *School of Life Sciences, Guangzhou University, #230 Waihuanxi Road, Guangzhou Higher Education Mega Center, Guangzhou 510006, China* **2** *School of Earth Sciences and Engineering, Sun Yat-sen University, Guangzhou 510275, China* **3** *College of Life Sciences, Capital Normal University, Xisanhuanbeilu 105, Haidian District, Beijing 100048, China*

Corresponding author: *Qiang Yang* (yq11_1984@126.com)

Academic editor: *Shaun Winterton* | Received 9 April 2019 | Accepted 24 June 2019 | Published 18 July 2019

http://zoobank.org/9F207A95-C905-444F-BB5D-19F69E9C7549

Citation: Yang Q, Shi C, Ren D (2019) A new genus and species of berothids (Insecta, Neuroptera) from the Late Cretaceous Myanmar amber. ZooKeys 864: 99–109. https://doi.org/10.3897/zookeys.864.35271

Abstract

A new genus and species of Berothidae is described from the Late Cretaceous (Cenomanian) Myanmar amber. *Ansoberotha jiewenae* **gen. et sp. nov.** can be easily distinguished from other berothid genera by the long antenna, the scape with ca. 100 flagellomeres, the forewing with four ra-rp, MPand CuA are pectinately branched, and the hind wing with one oblique cua-cup between CuA stem and the distal branch of CuP.

Keywords

Beaded lacewing, Burmese, fossil, long scape, Mesozoic

Introduction

Berothidae is a small family of Neuroptera, comprising approximately 110 extant species assigned to 24 genera, which were divided into six subfamilies (Aspöck and Randolf 2014, Oswald 2019). The family are distributed over all the biogeographic realms except for the Oceania and Antarctica. They are mainly restricted to the tropics and subtropics, with a few occurring in the temperate zone between 50°. Berothidae form a neuropteran

Copyright *Qiang Yang et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

clade with Rhachiberothidae and Mantispidae, although the phylogenetic relationships among the three families are still controversial (Tjeder 1959; Willmann 1990; Aspöck and Mansell 1994; Aspöck et al. 2001; Beutel et al. 2010; Zimmermann et al. 2011; Randolf et al. 2013, 2014; Aspöck and Randolf 2014; Haring and Aspöck 2004; Winterton et al. 2010; Engel et al. 2018). In particular, the disagreement on the familial status of Rhachiberothidae resulted in the questionable assignment of the extinct subfamily Paraberothinae (Nel et al. 2005; Makarkin and Kupryjanowicz 2010; Makarkin 2015). Herein, we tentatively follow the cladograms of Neuroptera in Wang et al. (2017), and exclude Rhachiberothidae including Paraberothinae from the family Berothidae.

Berothidae have a fossil history dating back to the Middle Jurassic. Approximately 22 genera with 33 species have been described, mainly distributed in the Eurasia, North and South America (as shown in Table 1). Among them, ten genera with 13 species have been described from the Myanmar amber, representing the most abundant and diverse morphology of the fossil berothids (Engel 2004; Engel and Grimaldi 2008; Yuan et al. 2016; Makarkin 2018; Huang et al. 2019). Herein, a new genus and species of Berothidae is described from the Late Cretaceous Myanmar amber.

Materials and methods

This study is based on one female specimen from Myanmar amber. The amber pieces were collected in the Hukawng Valley (the state of Kachin in northern Myanmar). A detailed map of the Hukawng Valley is given by Grimaldi et al. (2002: fig. 1). The volcanoclastic matrix of the amber is estimated to be ~98.79 ± 0.62 million years old, i.e., near the Albian/Cenomanian (Early/Late Cretaceous) boundary (Shi et al. 2012). The biological inclusions of Myanmar amber represent a sample of a tropical forest community in equatorial southeastern Asia at ~12°N paleolatitude (Grimaldi et al. 2002; Poinar et al. 2008; Zhang et al. 2018; Chen et al. 2019; Lin et al. 2019). The specimen was deposited by Ms Dan Zuo in the collections of the Key Laboratory of Insect Evolution & Environmental Changes, College of Life Sciences, Capital Normal University, Beijing, China (**CNUB**; Dong Ren, Curator). The specimen was examined using a Zeiss Discovery V20 stereomicroscope and photographed with an AxioCam HRc digital camera attached to the Zeiss Discovery V20 stereomicroscope (both instruments Carl Zeiss Light Microscopy, Göttingen, Germany). Line drawings were prepared with the Adobe Illustrator CS6 and with the aid of Adobe Photoshop CS6.

Venational terminology generally follows Kukalová-Peck and Lawrence (2004) as interpreted by Yang et al. (2012, 2014). Terminology of details of venation (e.g., spaces, veinlets, traces) follows Oswald (1993). Crossveins are designated after the longitudinal veins with which they connect and are numbered in sequence from the wing base.

Abbreviations:

AA1–AA3 first to third anterior anal vein;
CuA anterior cubitus;
CuP posterior cubitus;

Table 1. List of named fossil Berothidae.

Species	Age	Locality	Reference
Sinosmylites pectinatus Hong, 1983	Middle Jurassic Bathonian to Callovian	Inner Mongolia, China (Jiulongshan Formation)	Hong 1983
Sinosmylites fumosus Makarkin, Yang & Ren, 2011	Middle Jurassic Bathonian to Callovian	Inner Mongolia, China (Jiulongshan Formation)	Makarkin et al. 2011
Sinosmylites rasnitsyni Makarkin, Yang & Ren, 2011	Middle Jurassic Bathonian to Callovian	Inner Mongolia, China (Jiulongshan Formation)	Makarkin et al. 2011
Berothone protea (Panfilov, 1980)	Upper Jurassic Upper Callovian–Kimmeridgian	Karatau, Kazakhstan (Karabastau Formation)	Khramov 2015
Berothone gracilis (Panfilov, 1980)	Upper Jurassic Upper Callovian–Kimmeridgian	Karatau, Kazakhstan (Karabastau Formation)	Khramov 2015
Krokhathone parva Khramov, 2015	Upper Jurassic Upper Callovian–Kimmeridgian	Karatau, Kazakhstan (Karabastau Formation)	Khramov 2015
Krokhathone tristis Khramov, 2015	Upper Jurassic Upper Callovian–Kimmeridgian	Karatau, Kazakhstan (Karabastau Formation)	Khramov 2015
Sinosmylites karatavicus Khramov, 2015	Upper Jurassic Upper Callovian–Kimmeridgian	Karatau, Kazakhstan (Karabastau Formation)	Khramov 2015
Sinosmylites auliensis Khramov, 2015	Upper Jurassic Upper Callovian–Kimmeridgian	Karatau, Kazakhstan (Karabastau Formation)	Khramov 2015
Sinosmylites hotgoricus Khramov, 2015	Upper Jurassic	Khoutiyn-Khotgor, Mongolia (Ulan-Ereg Formation)	Khramov 2015
Epimesoberotha parva Jepson, Makarkin & Coram	Early Cretaceous Early Berriasian	Durlston Bay, England (Lulworth Formation)	Jepson et al. 2012
Banoberotha enigmatica Whalley, 1980	Early Cretaceous Valanginian/Hauterivian	Lebanese amber (Jezzine)	Whalley 1980
Sibelliberotha rihanensis Azar & Nel, 2013	Early Cretaceous Valanginian/Hauterivian	Lebanese amber (Jezzine)	Azar and Nel 2013
Oloberotha sinica Ren & Guo, 1996	Early Cretaceous Barremian	Liaoning, China (Yixian Formation)	Ren and Guo 1996
Ansoberotha jiewenae gen. & sp. n.	Late Cretaceous lowermost Cenomanian	Myanmar amber	This paper
Dasyberotha eucharis Engel & Grimaldi, 2008	Late Cretaceous lowermost Cenomanian	Myanmar amber	Engel and Grimaldi 2008
Ethiroberotha elongata Engel & Grimaldi, 2008	Late Cretaceous lowermost Cenomanian	Myanmar amber	Engel and Grimaldi 2008
Haploberotha carsteni Makarkin, 2018	Late Cretaceous lowermost Cenomanian	Myanmar amber	Makarkin 2018
Haploberotha persephone Engel & Grimaldi, 2008	Late Cretaceous lowermost Cenomanian	Myanmar amber	Engel and Grimaldi 2008
Iceloberotha kachinensis Engel & Grimaldi, 2008	Late Cretaceous lowermost Cenomanian	Myanmar amber	Engel and Grimaldi 2008
Iceloberotha simulatrix Engel & Grimaldi, 2008	Late Cretaceous lowermost Cenomanian	Myanmar amber	Engel and Grimaldi 2008
Jersiberotha myanmarensis Engel & Grimaldi, 2008	Late Cretaceous lowermost Cenomanian	Myanmar amber	Engel and Grimaldi 2008
Jersiberotha tauberorum Engel & Grimaldi, 2008	Late Cretaceous lowermost Cenomanian	Myanmar amber	Engel and Grimaldi 2008
Protoberotha minuta Huang, Ren & Wang, 2019	Late Cretaceous lowermost Cenomanian	Myanmar amber	Huang et al. 2019
Systenoberotha magillae Engel & Grimaldi, 2008	Late Cretaceous lowermost Cenomanian	Myanmar amber	Engel and Grimaldi 2008
Telistoberotha libitina Engel & Grimaldi, 2008	Late Cretaceous lowermost Cenomanian	Myanmar amber	Engel and Grimaldi 2008
Maculaberotha nervosa Yuan, Ren & Wang, 2016	Late Cretaceous lowermost Cenomanian	Myanmar amber	Yuan et al. 2016
Magniberotha recurrens Yuan, Ren & Wang, 2016	Late Cretaceous lowermost Cenomanian	Myanmar amber	Yuan et al. 2016
Jersiberotha luzzii Grimaldi, 2000	Late Cretaceous Turonian	Raritan (New Jersey) amber	Grimaldi 2000
Jersiberotha similis Grimaldi, 2000	Late Cretaceous Turonian	Raritan (New Jersey) amber	Grimaldi 2000
Nascimberotha picta Grimaldi, 2000	Late Cretaceous Turonian	Raritan (New Jersey) amber	Grimaldi 2000
Microberotha macculloughi Archibald & Makarkin, 2004	Early Eocene	Hat Creek amber, British Columbia	Archibald and Makarkin 2004
Elektroberotha groehni Makarkin & Ohl, 2015	Late Eocene	Baltic amber	Makarkin and Ohl 2015
Xenoberotha angustialata Makarkin, 2017	Early Eocene late Ypresian	Colorado, USA (Green River Formation)	Makarkin 2017

MA / MP	anterior and posterior branches of media;
RA	anterior radius;
RP	posterior radius;
RP1	proximal-most branch of RP;
RP2	branch of RP distal to RP1;
ScA	subcosta anterior;
ScP	subcosta posterior.

Systematic paleontology

Class Insecta Linnaeus, 1758
Order Neuroptera Linnaeus, 1758
Family Berothidae Handlirsch, 1906

Genus *Ansoberotha* gen. nov.
http://zoobank.org/A9486E3A-C995-430F-9D54-F45F1DC9279B

Type (and only) species. *Ansoberotha jiewenae* gen. et sp. nov.

Etymology. The generic name is a combination of the Latin *ansa* (meaning haft, handle), and *Berotha*, the type genus of the family, in reference to the long scapus. Gender feminine.

Diagnosis. Antenna long, more than 6.6 mm, longer than body or forewings; scape elongate, ca. 0.64 mm, almost 12 times as long as wide; flagellum with about 100 flagellomeres. Pronotum elongate, about three times as long as wide. Forewing with one basal sc-r and four ra-rp, M forked distal to the separation of RP; MP, CuA pectinately branched. Hind wing with one r-m between RP stem and MA; one oblique cua-cup between CuA stem and distal branch of CuP.

***Ansoberotha jiewenae* gen. et sp. nov.**
Figures 1, 2
http://zoobank.org/08878C7B-AC2C-48D8-BD01-824134515A83

Etymology. The specific epithet is named after Ms Jiewen Zhao (Hunan, China), the daughter of this amber's owner (Ms Dan Zuo). Her mother hopes that this honour will promote Jiewen's interests in natural history.

Diagnosis. As for the genus.

Holotype. CNU-NEU-MA2018072, female, a nearly complete and well-preserved specimen.

Locality and horizon. Hukawng Valley, Kachin State, northern Myanmar; lowermost Cenomanian, Upper Cretaceous.

Description. Holotype CNU-NEU-MA2018072. Total body length 4.0 mm. Head and body with numerous scattered, fine setae; head about as wide as long. Com-

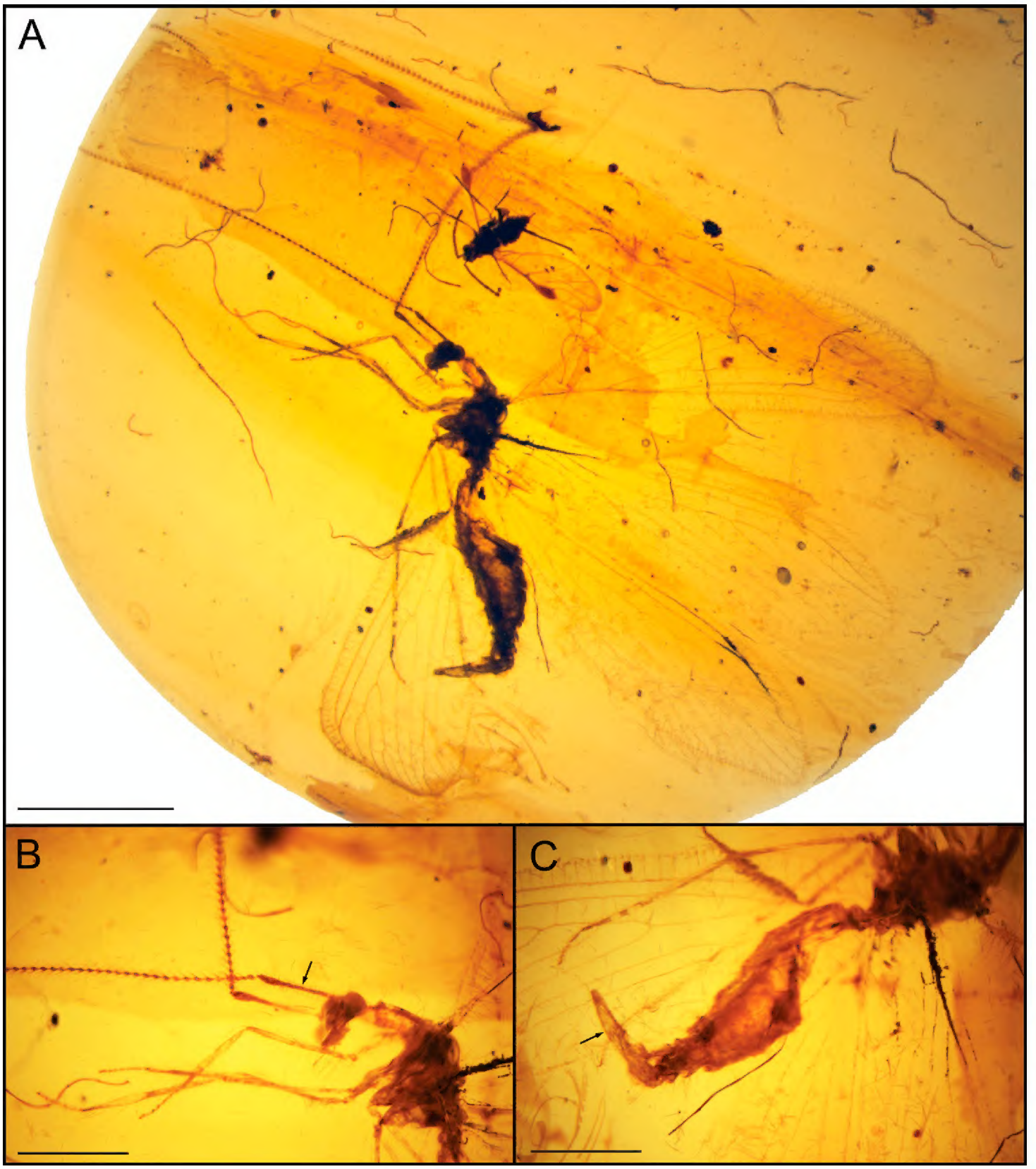

Figure 1. *Ansoberotha jiewenae* gen. et sp. nov., holotype CNU-NEU-MA2018072 **A** photograph of holotype **B** detailed photograph of antenna, arrow shows the long scape **C** detailed photograph of abdomen, arrow shows the gonapophysis lateralis. Scale bars 2 mm (**A**) and 1 mm (**B, C**).

pound eyes large. Antenna filiform, over 6.6 mm, with scattered setae all over; scape elongate, ca. 0.64 mm, almost 12 times as long as wide; pedicel as long as wide, slightly thicker than flagellum; flagellum with approximately 100 flagellomeres, the last few flagellomeres tapering. Pronotum elongate, narrower than head, about three times as long as wide; pro-, meso-, and metanotum with scattered, long, fine setae. Legs relatively long and slender, with numerous short setae intermixed with long setae. Forelegs: coxa elongated; femur long and slender; tibia slightly inflated nearly as long as femur; basitarsus nearly three times as long as the second tarsomere, the last four tarsomeres

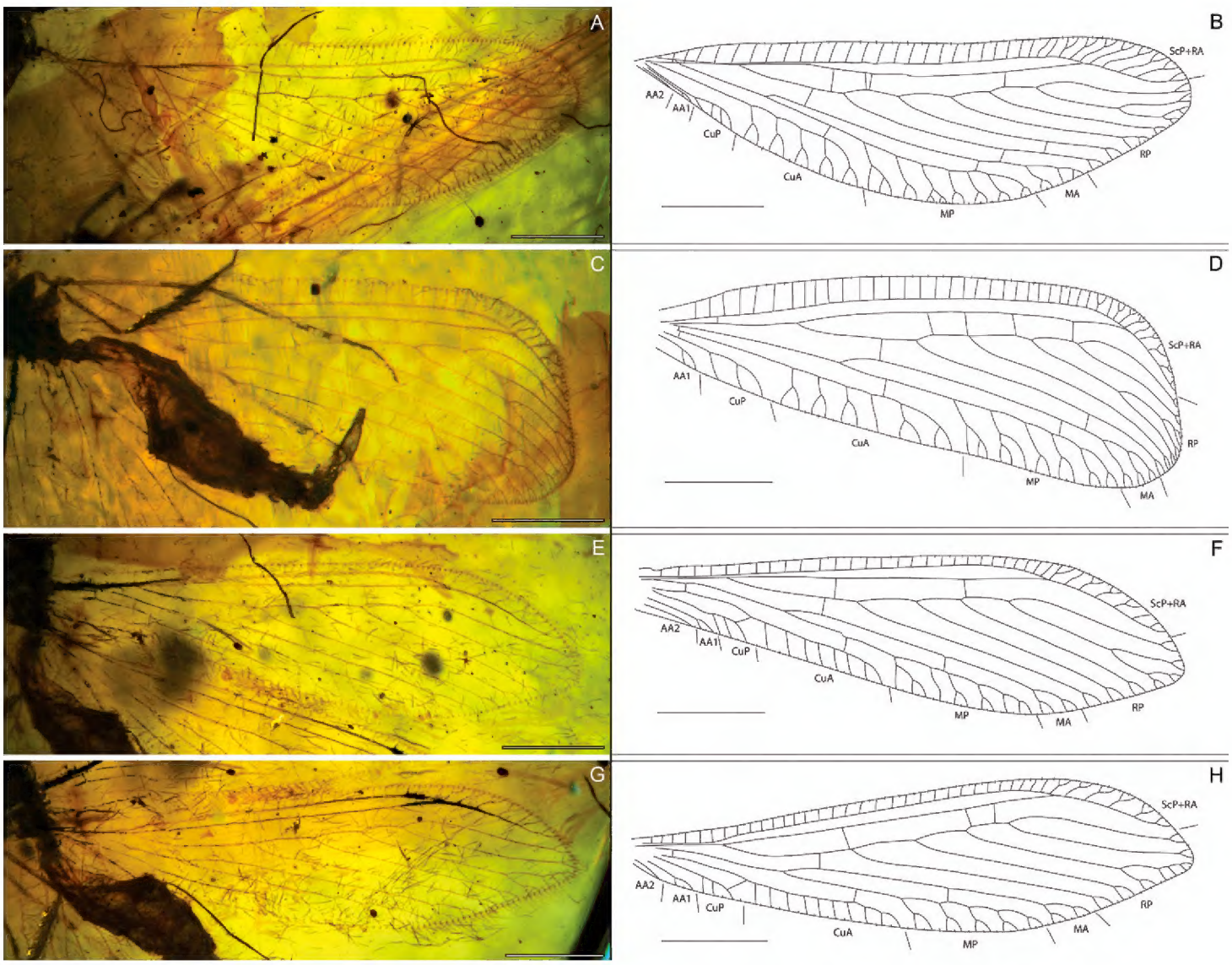

Figure 2. *Ansoberotha jiewenae* gen. et sp. nov., holotype CNU-NEU-MA2018072 **A, B** photograph of left forewing and line drawing **C, D** photograph of right forewing and line drawing **E, F** photograph of left hind wing and line drawing **G, H** photograph of right hind wing and line drawing. Scale bars 1 mm.

of the same length, each tarsomeres with two ended spur. Mid- and hind legs coxa coniform, thicker than forelegs. Each leg with two pretarsal claws, one big arolium. Abdomen nine segments, with scattered short setae; gonapophysis lateralis elongate.

Forewing length 5.5 mm, width 1.5 mm (left forewing/LFW); length 4.9 mm, width 1.8 mm (right forewing/RFW); elongated ovoid, apex rounded, with dense relatively short setae on veins and longer setae on margins; trichosors prominent along entire wing margin. Humeral vein crossvein-like; presumable ScA not detected; costal space relatively broad; most subcostal veinlets simple, not forked, only three (LFW) or four (RFW) distal apex subcostal veinlets forked once, pterostigma not present. ScP and RA fused distally, entering margin before wing apex; ScP+RA with five forked veinlets. Subcostal space slightly narrower than costal space, basally narrowed; only one sc-r present in right forewing, left forewing not detected due to preservation; four ra-rp crossveins located proximal to the fusion of ScP and RA. RP separated from R distal to sc-r, with six (LFW) or five (RFW) branches; RP4 (LFW) dichotomously forked, RP3 (RFW) pectinately forked, with three branches; only one crossveins detected between RP1, RP2 in LFW. M divided into MA and MP distal to the origin of RP and proximal to the separation of RP1 from RP stem, one ma-mp crossvein present; MA distally pectinately forked, with three branches; MP pectinately forked, with seven (LFW) or

six (RFW) branches; two crossveins between stem RP, MA and RP1, MA. Cu divided into CuA and CuP near wing base, with one m-cu detected in LFW, two in RFW; CuA pectinately forked, with five (LFW) or six (RFW) distal forked branches; CuP pectinately forked, with three or four simple branches, one crossvein between CuA, CuP in RFW detected. AA1 with a distal fork; AA2, AA3 not detected; no crossveins detected between AA region. Membrane without colour pattern.

Hind wing elongate, length 5.1 mm, width 1.5 mm (left hind wing/LHW); length 5.2 mm, width 1.5 mm (right hind wing/RHW). Trichosors prominent along entire wing margin. Costal space narrow, dilated distal to the fusion of ScP and RA; subcostal veinlets simple, widely spaced, pterostigma not present. Subcostal space no crossveins detected. ScP and RA fused distally, entering margin before wing apex; ScP+RA with seven (LHW) or five (RHW) veinlets, most with distal fork. RA space wider than subcostal space, with two (LHW) or three (RHW) ra-rp located proximal to the fusion of ScP and RA. RP originated slightly distal to wing base, with five pectinate branches, most forked distally; RP4 of LHW, RP3 of RHW dichotomously forked distally; no crossveins between RP branches; one r-m between RP stem and MA. M forked distal to origin of RP and proximal to the origin of RP1; MA dichotomously branched distally; MP pectinately forked, with six (LHW) or five (RHW) branches, most with distal fork; one ma-mp between MA and MP. Cu divided into CuA and CuP near wing base; with two m-cu detected, one near wing base, another located between RP and CuA branches; CuA long, parallel with the posterior margin, pectinately branched with eight (LHW) or 10 (RHW) simple branches; CuP with three distal simple pectinate branches; one oblique cua-cup between CuA stem and diatal branch of CuP. AA1 with a distal fork; AA2 simple; AA3 not detected; no crossveins detected between AA region. Membrane without colour pattern.

Remarks. *Ansoberotha* gen. nov. is distinctly different from the other Burmese amber berothid genera by having following characters: (1) *Ansoberotha* gen. nov. antenna is very long, over 6.6 mm, longer than body or forewings; the scape is elongate, ca. 0.64 mm, almost 12 times as long as wide; the flagellum with approximately 100 flagellomeres; other genera without such long antenna, scape, or so many flagellomeres; (2) the forewing of *Ansoberotha* gen. nov. with four ra-rp; *Ethiroberotha* and *Protoberotha* without ra-rp; *Haploberotha* and *Maculaberotha* with only one ra-rp; *Jersiberotha*, *Iceloberotha*, *Telistoberotha,* and *Dasyberotha* with two ra-rp; (3) the forewing MP and CuA are pectinately branched, with no less than five branches; (4) the hind wing of *Ansoberotha* gen. nov. with one oblique cua-cup between CuA stem and the distal branch of CuP; other genera do not have this crossvein.

Acknowledgements

We appreciate the valuable comments and useful suggestions on our manuscript from the editor (Dr. Shaun L. Winterton), the reviewer (Dr. Vladimir N. Makarkin), and another anonymous reviewer. We thank Ms Dan Zuo (Changsha, Hunan, China) for donated of the type specimen to us for study. This study was supported by National Natural Sci-

ence Foundation of China (grant nos. 41602014, 31501881, 31730087), Program for Changjiang Scholars and Innovative Research Team in University (grant no. IRT-17R75), Project of High-level Teachers in Beijing Municipal Universities (IDHT20180518), Scientific Research Foundation of Guangzhou University (69-18ZX10150).

References

Archibald SB, Makarkin VN (2004) A new genus of minute Berothidae (Neuroptera) from Early Eocene amber of British Columbia, Canada. Canadian Entomologist 136: 61–76. https://doi.org/10.4039/n03-043

Aspöck U, Mansell MW (1994) A revision of the family Rhachiberothidae Tjeder, 1959, stat. n. (Neuroptera). Systematic Entomology 19: 181–206. https://doi.org/10.1111/j.1365-3113.1994.tb00587.x

Aspöck U, Plant JD, Nemeschkal HL (2001) Cladistic analysis of Neuroptera and their systematic position within Neuropterida (Insecta: Holometabola: Neuropterida: Neuroptera). Systematic Entomology 26: 73–86. https://doi.org/10.1046/j.1365-3113.2001.00136.x

Aspöck U, Randolf S (2014) Beaded lacewings – a pictorial identification key to the genera, their biogeographics and a phylogenetic analysis (Insecta: Neuroptera: Berothidae). Deutsche Entomologische Zeitschrift 61: 155–172. https://doi.org/10.3897/dez.61.8850

Azar D, Nel A (2013) A new beaded lacewing from a new Lower Cretaceous amber outcrop in Lebanon (Neuroptera: Berothidae). In: Azar D, Engel MS, Jarzembowski E, Krogmann L, Nel A, Santiago-Blay J (Eds) Insect Evolution in an Amberiferous and Stone Alphabet. Proceedings of the 6th International Congress on Fossil Insects, Arthropods and Amber. Brill, Leiden and Boston, 111–130. https://doi.org/10.1163/9789004210714_009

Beutel RG, Friedrich F, Aspöck U (2010) The larval head of Nevrorthidae and the phylogeny of Neuroptera (Insecta). Zoological Journal of the Linnean Society 158: 533–562. https://doi.org/10.1111/j.1096-3642.2009.00560.x

Chen S, Deng SW, Shih CK, Zhang WW, Zhang P, Ren D, Zhu YN, Gao TP (2019) The earliest Timematids in Burmese amber reveal diverse tarsal pads of stick insects in the mid-Cretaceous. Insect Science https://doi.org/10.1111/1744-7917.12601

Engel MS (2004) Thorny lacewings (Neuroptera: Rhachiberothidae) in Cretaceous amber from Myanmar. Journal of Systematic Palaeontology 2: 137–140. https://doi.org/10.1017/S1477201904001208

Engel MS, Grimaldi DA (2008) Diverse Neuropterida in Cretaceous amber, with particular reference to the paleofauna of Myanmar (Insecta). Nova Supplementa Entomologica 20: 1–86.

Engel MS, Winterton SL, Breitkreuz LCV (2018) Phylogeny and evolution of Neuropterida: Where have wings of lace taken us? Annual Review of Entomology 63(1): 531–551. https://doi.org/10.1146/annurev-ento-020117-043127

Grimaldi DA (2000) A diverse fauna of Neuropterodea in amber from the Cretaceous of New Jersey. In: Grimaldi DA (Ed.) Studies on Fossil in Amber, with Particular Reference to the Cretaceous of New Jersey. Backhuys Publishers, Leiden, 259–303. https://doi.org/10.1021/ja00303a021

Grimaldi DA, Engel MS, Nascimbene PC (2002) Fossiliferous Cretaceous amber from Myanmar (Burma): its rediscovery, biotic diversity, and paleontological significance. American Museum Novitates 3361: 1–72. https://doi.org/10.1206/0003-0082(2002)361<0001:FCAFMB>2.0.CO;2

Handlirsch A (1906–1908) Die fossilen Insekten und die Phylogenie der rezenten Formen. Ein Handbuch für Palaeontologen und Zoologen. W Engelmann, Leipzig, 1430 pp. [issued in 1906 (1–640); 1907 (641–1140); 1908 (1120–1430)]

Haring E, Aspöck U (2004) Phylogeny of the Neuropterida: a first molecular approach. Systematic Entomology 29: 415–430. https://doi.org/10.1111/j.0307-6970.2004.00263.x

Hong Y (1983) Middle Jurassic fossil insects in North China. Geological Publishing House, Beijing, 223 pp. [in Chinese, English summary]

Huang S, Ren D, Wang YJ (2019) A new basal beaded lacewing (Neuroptera: Berothidae) from mid-Cretaceous Myanmar amber. Cretaceous Research 95: 1–7. https://doi.org/10.1016/j.cretres.2018.10.025

Jepson JE, Makarkin VN, Coram RA (2012) Lacewings (Insecta: Neuroptera) from the Lower Cretaceous Purbeck Limestone Group, Dorset, UK. Cretaceous Research 34: 31–47. https://doi.org/10.1016/j.cretres.2011.10.001

Khramov AV (2015) Jurassic beaded lacewings (Insecta: Neuroptera: Berothidae) from Kazakhstan and Mongolia. Paleontological Journal 49(1): 26–34. https://doi.org/10.1134/S0031030115010062

Klimaszewski J, Kevan DKM (1986) A new lacewing-fly (Neuroptera: Planipennia) from Canadian Cretaceous Amber, with an analysis of its fore wing characters. Entomological News 97: 124–132.

Krüger L (1923) Neuroptera succinica baltica. Die im baltischen Bernstein eingeschlossenen Neuroptera des Westpreussischen Provinzial-Museums (heute Museum für Naturkunde und Vorgeschichte) in Danzig. Stettiner Entomologische Zeitung 84: 68–92.

Kukalová-Peck J, Lawrence JF (2004) Relationships among coleopteran suborders and major endoneopteran lineages: evidence from hind wing characters. European Journal of Entomology 101: 95–144. https://doi.org/10.14411/eje.2004.018

Lin XD, Labandeira CC, Shih CK, Hotton LC, Ren D (2019) Life habits and evolutionary biology of new two-winged long-proboscid scorpionflies from mid-Cretaceous Myanmar amber. Nature Communications https://doi.org/10.1038/s41467-019-09236-4

Linnaeus C (1758) Systema naturae per regna tria naturae secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 10th Edition. Vol. 1. Salvii, Holmiae, 824 pp. https://doi.org/10.5962/bhl.title.542

Makarkin VN (1994) Upper Cretaceous Neuroptera from Russia and Kazakhstan. Annales de la Societe Entomologique de France 30(3): 238–292.

Makarkin VN (2015) A new genus of the mantispid-like Paraberothinae (Neuroptera: Berothidae) from Burmese amber, with special consideration of its probasitarsus spine-like setation. Zootaxa 4007(3): 327–342. https://doi.org/10.11646/zootaxa.4007.3.2

Makarkin VN (2017) An interesting new genus of Berothinae (Neuroptera: Berothidae) from the early Eocene Green River Formation, Colorado. Zootaxa 4226(4): 594–600. https://doi.org/10.11646/zootaxa.4226.4.9

Makarkin VN (2018) A new species of *Haploberotha* (Neuroptera: Berothidae) from mid-Cretaceous Burmese amber. Cretaceous Research 90: 375–381. https://doi.org/10.1016/j.cretres.2018.06.011

Makarkin VN, Kupryjanowicz J (2010) A new mantispid-like species of Rhachiberothinae from Baltic amber (Neuroptera, Berothidae), with a critical review of the fossil record of the subfamily. Acta Geologica Sinica 84: 655–664. https://doi.org/10.1111/j.1755-6724.2010.00238.x

Makarkin VN, Ohl M (2015) An important new fossil genus of Berothinae (Neuroptera: Berothidae) from Baltic amber. Zootaxa 3946(3): 401–415. https://doi.org/10.11646/zootaxa.3946.3.7

Makarkin VN, Yang Q, Ren D (2011) Two new species of *Sinosmylites* Hong (Neuroptera: Berothidae) from the Middle Jurassic of China, with notes on Mesoberothidae. ZooKeys 130: 199–215. https://doi.org/10.3897/zookeys.130.1418

Nel A, Perrichot V, Azar D, Néraudeau D (2005) New Rhachiberothidae (Insecta: Neuroptera) in Early Cretaceous and Early Eocene ambers from France and Lebanon. Neues Jahrbuch für Geologie und Paläontologie Abhandlungen 235: 51–85. https://doi.org/10.2113/gsmicropal.51.6.487

Oswald JD (1993) Revision and cladistic analysis of the world genera of the family Hemerobiidae (Insecta: Neuroptera). Journal of the New York Entomological Society 101: 143–299. http://biostor.org/reference/41781

Oswald JD (2019) Neuropterida Species of the World. Version 6.0. http://lacewing.tamu.edu/SpeciesCatalog/Main [accessed 2019.04.01]

Poinar Jr GO, Buckley R, Brown AE (2008) The secrets of Burmite amber. MAPS Digest 20: 20–29.

Randolf S, Zimmermann D, Aspöck U (2013) Head anatomy of adult *Sisyra terminalis* (Insecta: Neuroptera: Sisyridae) – functional adaptations and phylogenetic implications. Arthropod Structure and Development 42: 565–582. https://doi.org/10.1016/j.asd.2013.07.004

Randolf S, Zimmermann D, Aspöck U (2014) Head anatomy of adult *Nevrorthus apatelios* and basal splitting events in Neuroptera (Neuroptera: Nevrorthidae). Arthropod Systematics and Phylogeny 72(2): 111–136.

Ren D, Guo ZG (1996) On the new fossil genera and species of Neuroptera (Insecta) from the Late Jurassic of northeast China. Acta Zootaxonomica Sinica 21: 461–479.

Shi GH, Grimaldi DA, Harlow GE, Wang J, Wang J, Yang MC, Lei WY, Li QL, Li XH (2012) Age constraint on Burmese amber based on UePb dating of zircons. Cretaceous Research 37: 155–163. https://doi.org/10.1016/j.cretres.2012.03.014

Tjeder B (1959) Neuroptera-Planipennia. The Lace-wings of Southern Africa. 2. Family Berothidae. In: Hanstrom B, Brinck P, Rudebec G (Eds) South African animal life. Vol. 6. Swedish Natural Science Research Council, Stockholm, 256–314.

Wang YY, Liu XY, Garzón-Orduña IJ, Winterton SL Yan Y, Aspöck U, Aspöck H, Yang D (2017) Mitochondrial phylogenomics illuminates the evolutionary history of Neuropterida. Cladistics 33: 617–636. https://doi.org/10.1111/cla.12186

Whalley PES (1980) Neuroptera (Insecta) in amber from the Lower Cretaceous of Lebanon. Bulletin of the British Museum of Natural History (Geology) 33: 157–164.

Willmann R (1990) The phylogenetic position of the Rhachiberothinae and the basal sister-group relationships within the Mantispidae (Neuroptera). Systematic Entomology 15: 253–265. https://doi.org/10.1111/j.1365-3113.1990.tb00316.x

Winterton SL, Hardy NB, Wiegmann BM (2010) On wings of lace: phylogeny and Bayesian divergence time estimates of Neuropterida (Insecta) based on morphological and molecular data. Systematic Entomology 35: 349–378. https://doi.org/10.1111/j.1365-3113.2010.00521.x

Yang Q, Makarkin VN, Winterton SL, Khramov AV, Ren D (2012) A remarkable new family of Jurassic insects (Neuroptera) with primitive wing venation and its phylogenetic position in Neuropterida. PLoS ONE 7(9): e44762. https://doi.org/10.1371/journal.pone.0044762

Yang Q, Makarkin VN, Ren D (2014) Two new species of *Kalligramma* Walther (Neuroptera: Kalligrammatidae) from the Middle Jurassic of China. Annals of the Entomological Society of America 107: 917–925. https://doi.org/10.1603/AN14032

Yuan DD, Ren D, Wang YJ (2016) New beaded lacewings (Neuroptera: Berothidae) from Upper Cretaceous Burmese amber. Cretaceous Research 68: 40–48. https://doi.org/10.1016/j.cretres.2016.08.007

Zhang WT, Li H, Shih CK, Zhang AB, Ren D (2018) Phylogenetic analyses with four new Cretaceous bristletails reveal inter-relationships of Archaeognatha and Gondwana origin of Meinertellidae. Cladistics 34: 384–406. https://doi.org/10.1111/cla.12212

Zimmermann D, Randolf S, Metscher BD, Aspöck U (2011) The function and phylogenetic implications of the tentorium in adult Neuroptera (Insecta). Arthropod Structure and Development 40: 571–582. https://doi.org/10.1016/j.asd.2011.06.003